

POLLINATOR MAINTENANCE VS. FRUIT PRODUCTION: PARTITIONED REPRODUCTIVE EFFORT IN SUBDIOECIOUS *FUCHSIA LYCIOIDES*

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ABSTRACT

Populations of *Fuchsia lycioides* Andrews are composed of small-flowered female plants and an equal number of larger-flowered hermaphrodites, which may be female fertile, or morphologically or physiologically female sterile. A major selective force driving the evolution of separate sexes in *F. lycioides* is suggested to be the partitioning of limited resources associated with pollinator maintenance and fruit production in a semi-arid mediterranean climate. The hummingbird *Rhodopsis vesper atacamensis* is the only known pollinator, and appears to be energetically dependent upon *F. lycioides*. Hermaphrodites are facultative in their fruit production, produce as much as six times more nectar than females, and feed birds both prior to flower opening and during anthesis. Females bear abundant fruit and produce only a relatively small amount of nectar during anthesis. Nectar production is extremely variable in both sexes but is unpredictable in hermaphrodites and apparently predictable in females. The unpredictability of hermaphrodite nectar production may be a key factor permitting the evolution of resource partitioning into large-flowered bird-feeding pollen plants and small-flowered reproductive individuals.

Subdioecy, a state of dioecy in which populations regularly contain imperfectly differentiated individuals in addition to strictly unisexual individuals, has evolved by at least five evolutionary pathways (Ross, 1982). The genus *Fuchsia* is characterized by the hermaphroditism–gynodioecy–subdioecy pathway, wherein the male sterile mutants among the hermaphrodites produce the gynodioecious state, followed by a gradual reduction of seed fertility of hermaphrodites so that these come to function largely or completely as males (Godley, 1955; Breedlove, 1969; Arroyo & Raven, 1975).

The selective forces apparently responsible for the evolution of dioecy have recently been reviewed by Ross (1982), who emphasized that many of the proposed selection models (fertility variation, sexual selection, overdominance, and resource allocation) are scarcely or not at all distinct from each other. Cases involving pollinator influence, fruit dispersal, and predation (Bawa, 1980; Givnish, 1980) are also likely to involve differential resource allocation. If so, perhaps the most generalized model for the evolution of dioecy is simply an energetic argument: that female reproductive effort is largely limited by the availability of physiological resources, and that separation of the sexes increases fitness by allowing more efficient use or allocation of limiting factors. The resource allocation model need not exclude the traditionally considered hypothesis of outbreeding advantage (inbreeding depression). Ross (1982) concludes that outbreeding advantage is not always a factor in the evolution of dioecy, and even where it occurs, it is probably accompanied by other selective forces. Freeman et al. (1980a), and Bawa (1980) have expressed similar views.

In this paper we report observations on the floral biology of a facultatively

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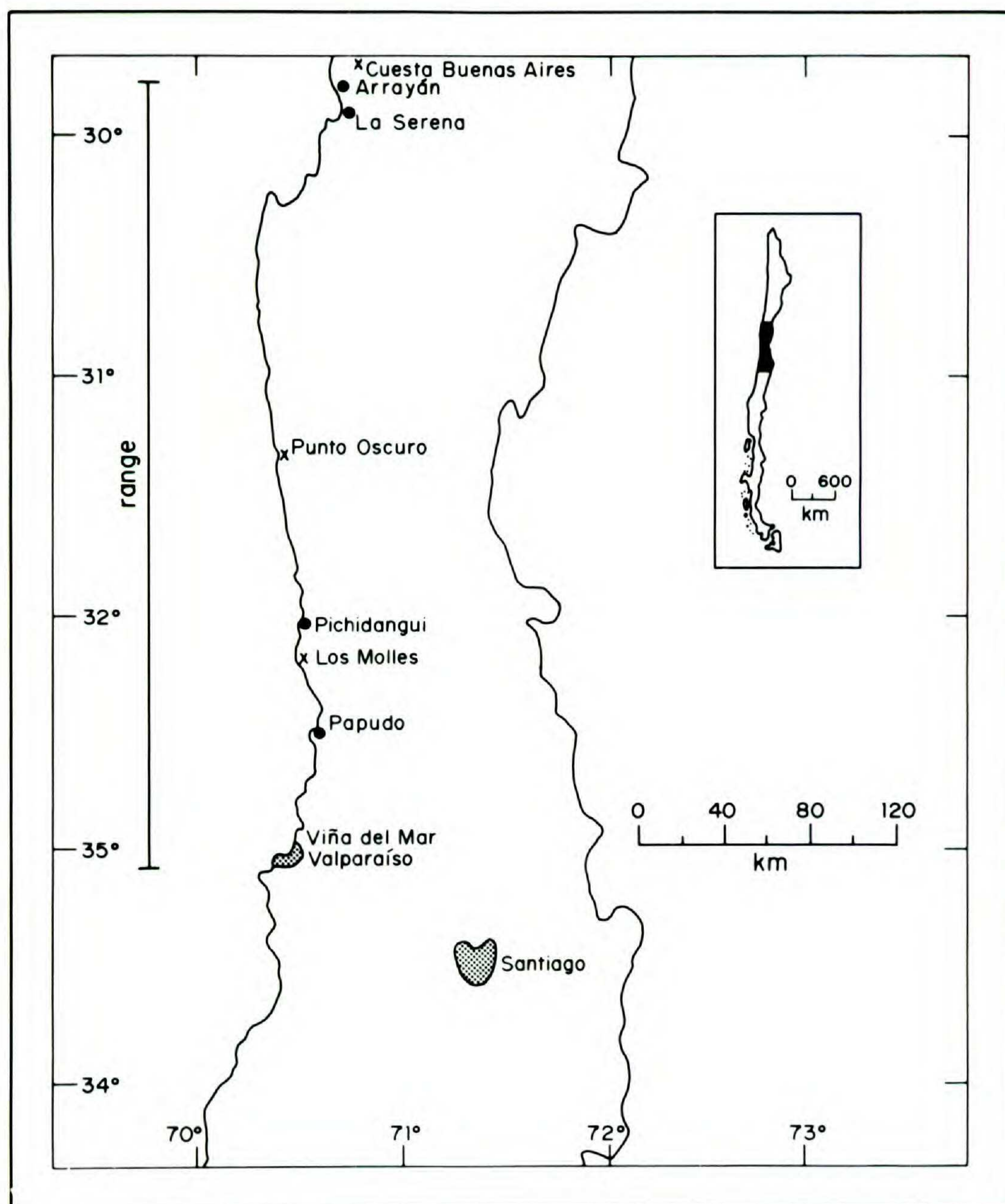


FIGURE 1. The geographic range of *Fuchsia lycioides* and the location of study sites along the coast of central Chile.

subdioecious shrub, *Fuchsia lycioides* Andrews, and examine evidence consistent with the hypothesis that differential resource allocation (related to pollinator maintenance) may be an important selective force favoring the evolution of separate sexes in this species.

Fuchsia lycioides, forming the monotypic section *Kirschlegeria* of the genus, is restricted to a narrow coastal belt in the Mediterranean-climate zone of central Chile (Fig. 1) in a relatively severe environmental regime with only moderate winter precipitation and long dry summer conditions. At its southern limit south of Valparaíso, mean annual precipitation is 460 mm/yr while at its northern limit north of La Serena there is only slightly more than 150 mm/yr. Mean growing season temperatures vary little over this latitudinal range.

Ecologically, *F. lycioides* is characteristic of bluff communities along the immediate coast where it occurs in mixed stands of deciduous and evergreen shrub

species. On typical sites such as those at Pichidangui (Coquimbo Province) it occurs with other woody deciduous shrubs (*Adesmia arborea* and *Proustia pungens*), a mixed assemblage of deciduous semiwoody shrubs, and the evergreen *Lithraea caustica*. On exposed rocky headlands, as at Los Molles (Aconcagua Province) just south of Pichidangui, however, *F. lycioides* occurs in a predominately evergreen community dominated by *Lucuma valparadisea*. Further north at Punto Oscuro, and near La Serena, it occurs in a community strongly dominated by the shrubby *Oxalis gigantea*, a desert floristic element. In all of these varied community types, *F. lycioides* remains an important (dominant) species.

METHODS

Field observations and data were collected over the entire range of the species in Chile, at Papudo, Los Molles, Pichidangui, Punto Oscuro, Arrayan, and Cuesta Buenos Aires, in the years 1974, 1975, 1977, and 1978. Differences between hermaphrodite and female flowers were characterized by measuring flower tube length and style length in one southern (Pichidangui) and one northern (Arrayan) population. Data were also collected on style abortion in hermaphrodites, and the ratio of female to hermaphrodite individuals was determined at four sites.

The standing nectar crop was measured by sampling flowers with 10 μ l micropipets. In the field, buds were sampled in late afternoon by puncturing the base of the closed flower tube with a micropipet. Open, non-pollinated flowers (lacking white pollen on the red stigma) were sampled between 800 and 1000 hours. Nectar was measured for a series of marked flowers in the late afternoon, and the flowers were then bagged and remeasured the following morning to determine overnight nectar production. Nectar productivity was also measured from three plants each of female and hermaphrodite individuals raised from seed in the greenhouse. Flowers were tagged and measured at 1700 hours on the first, second, and third day after opening.

RESULTS

FLORAL BIOLOGY

The rose-colored, dimorphic flowers of *F. lycioides* have four sepals, four small petals, and a cylindric floral tube. The open cup-shaped floral tube of the female flower is usually 1.5–3 mm long, with a 6–10 mm style at our primary study site at Pichidangui. Eight reduced anthers are present but do not contain pollen. The larger hermaphrodite flowers are 2.5–5 mm long, with style length ranging from 14–22 mm. Although tube length of the two flower types may occasionally overlap, there is a sharp gap of 3.5–4 mm between maximum style length in the small female flowers and minimum style length in the larger hermaphrodite flowers (Fig. 2). Flowers of the Arrayan population show the same pattern but are smaller in size, particularly with regard to maximum style length, reflecting the considerably drier conditions under which these plants were growing.

A variable proportion of the flowers on hermaphrodite plants lack styles and are therefore functionally male. The percentage of male flowers on hermaphrodite plants was quantified in the northern Arrayan and Cuesta Buenos Aires popula-

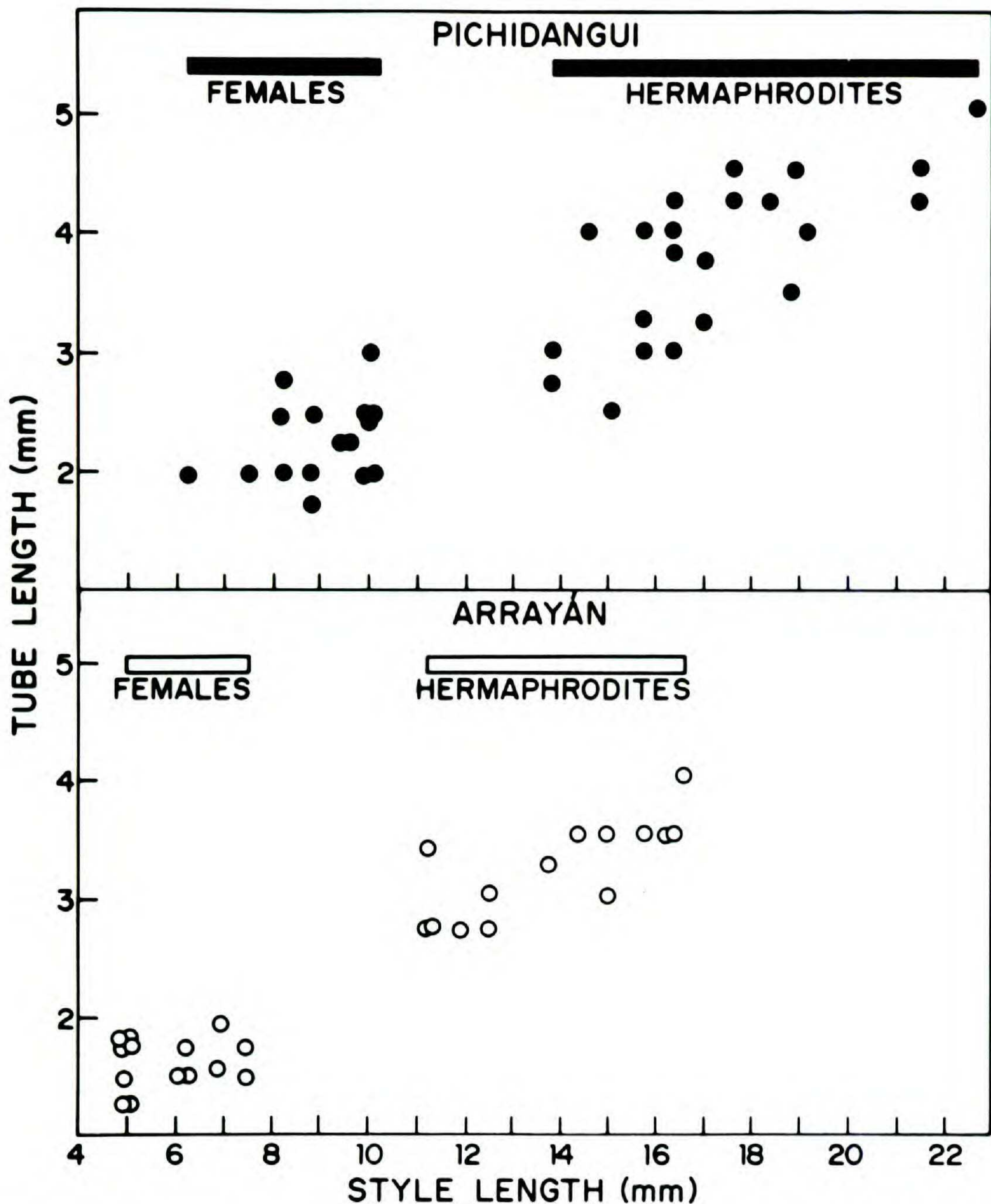


FIGURE 2. Flower size in a northern and southern population of *Fuchsia lycioides*. Note that the style lengths of hermaphrodites and females are variable but well separated.

tions by recording the proportion of aborted styles in ten randomly chosen flowers on each of 28 "hermaphrodite" individuals (Fig. 3). One-quarter of these plants had all perfect flowers. In the remaining individuals the percentage of male flowers ranged from 10 to 100%. Although similar data were not collected at the southern Pichidangui population, the frequency of individuals with high proportions of flowers with aborted styles was observed to be very low. The Pichidangui site is considerably more mesic than the northern population, suggesting that style condition may be influenced by moisture stress.

Perhaps the most striking difference between female and hermaphrodite individuals, other than flower size, was the presence of abundant fruit on female plants and its general absence on hermaphrodites. At Pichidangui, for example, all female plants sampled in 1974 produced fruit, with a mean of 11.4 berries per new shoot. In contrast, 81% of 26 hermaphrodites sampled produced no fruit,

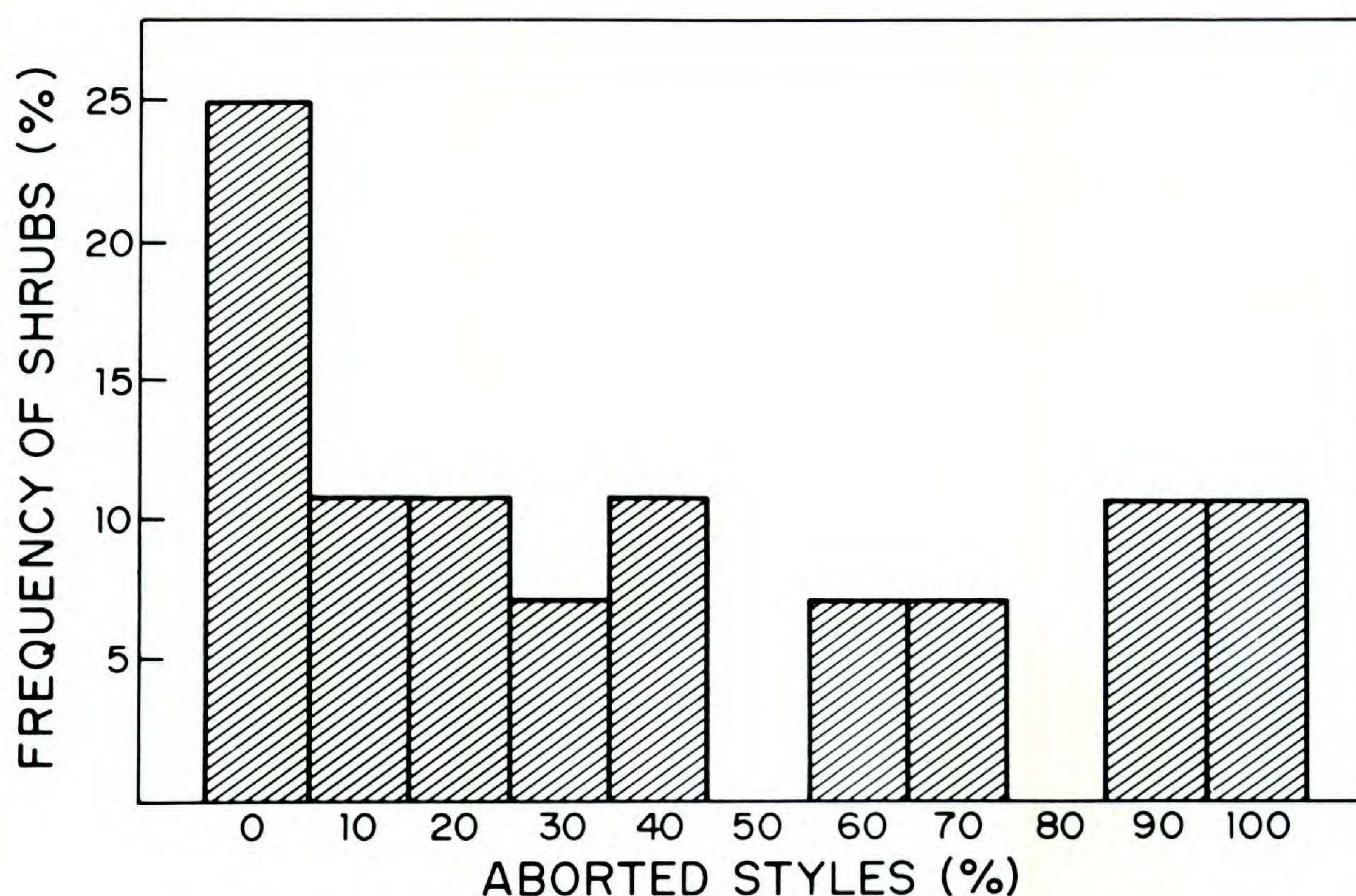


FIGURE 3. The percentage of male flowers (aborted styles) on hermaphrodite plants in the northern Arrayan and Cuesta Buenos Aires populations.

and the remainder bore only a small number per plant. These were positioned in the axils of new shoots, suggesting that they were produced very early in the growing season, before shoot expansion occurred. Similar patterns of fruit production were observed at nearby Los Molles, and the northern Arrayan and Cuesta Buenos Aires sites. However, at Punto Oscuro in the central part of the species range, a single large population was sampled in which a majority of the hermaphrodites bore abundant fruit in 1974. The seeds within the hermaphrodite berries were normal with respect to both quality and quantity, and readily germinated when later planted.

The ratio of hermaphrodite to female individuals is not different from expected frequencies based on a 50:50 sex ratio for all sites (all χ^2 s between 0.04 and 0.190). The percentage hermaphrodites and sample sizes were: Pichidangui 51%, $n = 100$; Papudo 48%, $n = 50$; Arrayan 53%, $n = 41$; Cuesta Buenos Aires 53%, $n = 53$. The sexes showed no apparent differences in microhabitat distribution, although this was not quantified beyond our estimation that similar proportions of each sex occurred in the small homogeneous areas we examined.

POLLINATION

The only known pollinator of *F. lycioides* is a small, extremely timid hummingbird, *Rhodopsis vesper atacamensis* Leybold. This small-billed race (22.9 mm) of the larger northern subspecies (bill length 30.7 mm) is known only from the coastal areas inhabited by *F. lycioides*, and appears to be largely energy dependent upon this species. There is an interesting similarity between bill length in *Rhodopsis vesper atacamensis* and maximum style length of *Fuchsia lycioides*

TABLE 1. Hermaphrodite flower piercing and pollination at three sites.

	(N)	Number of Buds Pierced	Number Pierced Flowers Polli- nated	Total Number Flowers Polli- nated	% Buds Pierced	% Pierced Flowers Polli- nated	% Total Flowers Polli- nated
Pichidangui	(279)	70	64	229	25	91	82
Pichidangui canyons	(21)	13	9	13	62	69	62
Papudo	(76)	69	33	37	91	48	49

(Fig. 2). At Pichidangui, hummingbird activity was observed only prior to 1000 hours, along the margins of the coastal headlands, and again in the late afternoon on the steep canyon slopes facing the sea. During morning activity the birds visit numerous flowers per plant, and move rapidly between hermaphrodite and female individuals with no obvious pattern of foraging or territoriality.

A consistent feature of flowers from all populations was the common presence of a hole at the base of the floral tube, attributable to piercing activity by *Rhodopsis*. Although we did not witness piercing, buds tagged in midafternoon were pierced by 10 am the following day. No insect other than an occasional honeybee was ever observed in or about the flowers. A few honeybees were found gathering pollen from hermaphrodite flowers, but their visits were easily distinguished by the presence of stringy masses of pollen hanging from the style and stigma. Honeybees were never observed at female flowers, which are also occasionally pierced. No evidence of chewing by bees or other insects was found in hundreds of observations. Bud piercing appears to occur chiefly in the evening since the rim of the pierced hole is discolored by the time the flower opens the following day. Piercing activity is predominately but not exclusively associated with the larger hermaphroditic buds.

The frequency of hermaphrodite piercing at three sites and its apparent relationship to pollination efficiency is given in Table 1. On the bluffs at Pichidangui, where a massive number of flowers were available in 1974, only one-quarter of the hermaphrodite flowers were pierced. Nevertheless, nearly all (91%) of these pierced buds received a return visit after opening, as evidenced by the presence of pollen on the stigmas of flowers with discolored holes. In the more protected canyons below these bluffs, 62% of the hermaphrodite flowers were pierced, but only 69% of these received return visits effecting pollination. At Papudo, where nearly all hermaphrodite flowers were pierced, hermaphrodite pollination dropped to 48%. Female flowers were rarely pierced at Pichidangui, but at Papudo, where 91% of all hermaphrodites were pierced, 27% of the small female flowers also had holes at the base of the floral tube. Comparison of the three sites suggests that overall pollination activity (return visits to open flowers) decreases significantly as the frequency of piercing increases. Despite considerable site variation in the frequency of flower piercing (25–91%) and total pollination (82–49%), the frequency of pollination of pierced flowers does not differ significantly from the frequency for unpierced flowers, demonstrating that individuals providing bud nectar are not at a selective disadvantage as pollen donors.

TABLE 2. Standing nectar crop (field) and productivity (greenhouse) of hermaphrodite and female flowers. Data in μ l.

		Hermaphrodite			Female		
		n	Mean	Range	n	Mean	Range
Field	Mature buds	18	1.72	0–3.6	12	0.21	0–0.8
	Day 1 flowers	155	1.88	0–7.0	70	0.80	0–2.9
Greenhouse	Day 1	10	3.81	0–6.2	9	1.10	0–1.6
	2	10	1.84	0–3.2	9	0.00	—
	3	10	0.76	0–1.8	9	0.00	—
	Total		6.41			1.10	

NECTAR PRODUCTION

Hermaphrodite flowers produce an average total of six times more nectar than do female flowers under greenhouse conditions (Table 2); they yield approximately 1.8 μ l per 24 hour period, beginning 12–36 hr before flower opening, and continuing for two days thereafter. Nectar productivity drops to 0.76 μ l on the third day after opening, and flowers usually wilt the next day. Female flowers produce very little nectar in bud, contain approximately 1 μ l at the end of the first day after opening, and then usually cease to produce nectar. Maximum yields sometimes reach 2 μ l (Fig. 4).

Variation in nectar production is the most striking and consistent feature observed in both field and greenhouse samples (Fig. 4). In the field, we found it impossible to predict nectar availability in hermaphrodite flowers using size, color, developmental state, and stigma condition as indicators (only flowers without pollen on the stigma were sampled). All plants produced nectarless flowers, plus flowers of low, intermediate, and high productivity. The greenhouse sampling demonstrated a similar pattern. Although females also produce nectarless flowers, nectar availability can nevertheless be assessed visually, since the eight large anthers that block the entrance to hermaphrodite flowers are absent. In contrast to the pendulous hermaphrodite flowers, the female flowers are held upright or at right angles to the ground, and the nectar is easily visible when the short floral tube is filled.

DISCUSSION

Fuchsia lycioides represents one of four instances in the genus *Fuchsia* in which male sterility has arisen independently in a small section with a distribution marginal to that of the genus as a whole (Raven, 1979). Floral morphology is misleading in this species and functional sex requires a physiological rather than a morphological definition (Ross, 1982). The female plants retain a set of small sterile anthers, and the hermaphrodite individuals produce two morphological types, perfect flowers, and styleless flowers. Superimposed on this morphological pattern is that fact that perfect flowers can also be female sterile. Both morphological and physiological female sterility may be influenced by environmental stress. Aborted styles were rarely observed at Pichidangui, but the absence of styles was a noticeable feature in the more northern, drier sites. However, even

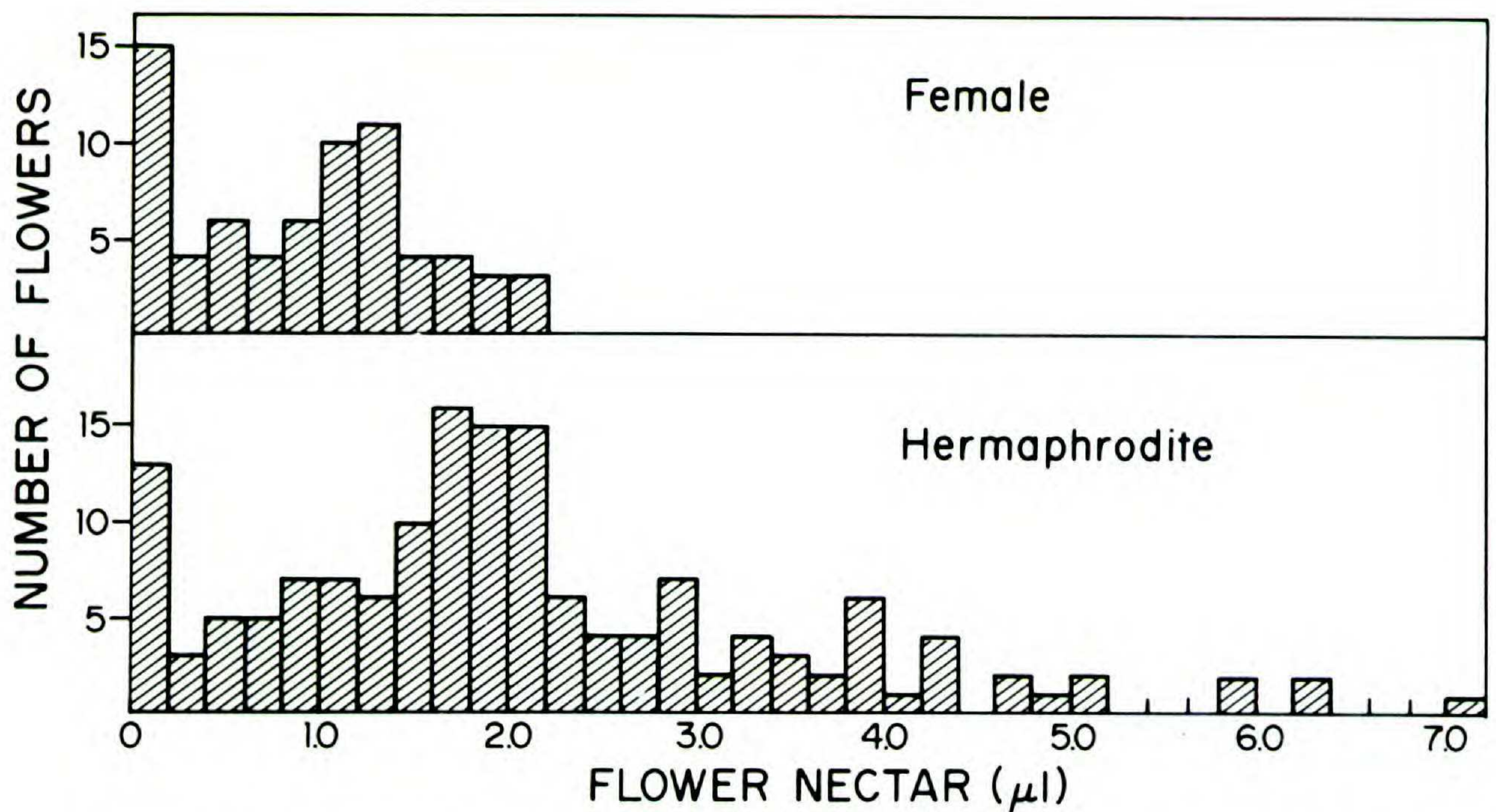


FIGURE 4. The standing nectar crop in open, non-pollinated non-pierced flowers at Pichidangui, a site with high flower density.

individuals with 100% styleless flowers on the date of our sample in 1974 bore a few fruits, demonstrating that the proportion of obligate male flowers changes seasonally. Individuals of many dioecious and subdioecious species are able to alter their sexual state in response to changes in the ambient environment and/or changes in size or age (Freeman et al., 1980b). Temperature is known to affect female fertility in perfect hermaphrodites of other gynodioecious *Fuchsias* (Arroyo & Raven, 1975). Under greenhouse conditions hermaphrodites of *F. thyifolia* and *F. microphylla* that were normally female sterile throughout the spring and summer months produced some fruit by self-pollination when greenhouse temperatures were lower at the onset of winter. A similar mechanism could account for the few scattered fruits found on hermaphrodites in most populations of *F. lycioides* early in the growing season. Examination of herbarium specimens and reports from local residents suggest that at least some individuals of *F. lycioides* may be in flower from August through April, with some evidence existing for distinct peaks in flowering at irregular intervals. This condition may be related to precipitation patterns. Late in the season, particularly from January to April, flowering may be confined to a few individual branches on a shrub, indicating physiological compartmentalization of phenological development. Few other associated species are able to flower under the water stress conditions of this summer period. We do not know if *Rhodopsis* is present throughout the year.

Although we observed what appeared to be indiscriminate visitation to both sexes by *Rhodopsis*, it was not immediately clear why the bird should visit female plants when hermaphrodites were available. However, if *Rhodopsis* is no more efficient than we were when foraging at hermaphrodite flowers, the increased cost of searching time within large-flowered plants may significantly reduce the benefits gained when large nectar strikes occur. Within small-flowered plants, the bird should be able to recognize full floral tubes and therefore consistently forage

at flowers with a time/energy yield equal to or greater than the average productivity of the unpredictable hermaphrodites. A system with inequality of nectar production appears to function only because each hermaphrodite flower must be sampled to detect its variable reward, while this may not be true for open, upright female flowers.

Bud piercing is presumed to be an indicator of energetic stress in *Rhodopsis*, since its frequency varies with resource concentration. At Pichidangui, where shrub and flower densities were very high, flower piercing was relatively low and most flowers were visited legitimately (Table 1). Bud piercing increased in Pichidangui canyons, where individual plants were widely separated, and at Papudo, where flower production was very low. The lower pollination efficiency associated with reduced availability of bud nectar (Table 1) suggests that *Rhodopsis* is forced to decrease its foraging time in populations lacking this energy supplement.

Lloyd & Webb (1977) argued that male reproduction effort is likely to be less than that of females, unless extraordinary quantities of pollen are required either to achieve high fertilization levels or for indirect contributions to fitness such as pollinator rewards. We believe that pollinator maintenance may be a pivotal condition for the persistence of *F. lycioides* in its present arid environment, and thus a major selective force driving this species toward functional dioecy. Bird pollination is rare among dioecious species (Bawa, 1980), perhaps because energetically expensive pollination systems are selected against if nectar production and ovules utilize the same resources and limit each other's production within the female. Under these conditions selection for decreased energy allocation to nectar (by shifting to small insect pollination) might be expected to precede or evolve concurrently with dioecy. Indeed, such a shift appears to have occurred in the gynodioecious and dioecious *Fuchsias* that inhabit temperate and cool-temperate mountain forests in Mexico and Central America. Four species attract both bees and hummingbirds, but bees (primarily *Bombus*) appear to be the more frequent visitors. Three taxa have shifted from having red flowers to having smaller white flowers and are pollinated solely by long-tongued tachinid flies (Table 1 in Breedlove, 1969). This option has apparently been unavailable on the coastal bluffs of central Chile, where potential insect pollinators are scarce. Although relatively calm conditions prevail during the early morning and late afternoon, strong on-shore winds occur during most of the day, making it extremely difficult for most pollinators to forage. *Fuchsia lycioides* is apparently forced to maintain a high-energy-requiring pollinator at a cost that directly competes with the energy demands of fruit production in an environment with low and unpredictable winter precipitation and long summer droughts. The solution would appear to be the evolution of resource partitioning into large-flowered bird-maintaining pollen plants and small-flowered reproductive individuals. This hypothesis explains the disproportionately greater daily nectar production of hermaphrodites and the coincident development of female sterility by these individuals.

Male-predominant sex ratios are a pronounced feature of many long-lived dioecious species. Most such skewed ratios are thought to be caused by higher female mortality rates, specifically, differential post-reproductive mortality associated with differences in reproductive effort (Lloyd, 1973; Lloyd & Webb,

1977). The numerical equality of the sexes in *F. lycioides* is consistent with our contention that each makes a functionally separate but energetically similar contribution to reproductive effort. While a resource partitioning hypothesis appears attractive in this case, this argument does not necessarily exclude nor diminish the importance of outcrossing enforcement as one of several factors contributing to the evolution of subdioecy in *F. lycioides*.

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